The Posterior Border of the Sphenoid Greater Wing and Its Phylogenetic Usefulness in Human Evolution

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ABSTRACT The elucidation of patterns of cranial skeletal maturation and growth in fossil hominids is possible not only through dental studies but also by mapping different aspects of ossification in both extant African apes and humans. However, knowledge of normal skeletal development in large samples of extant great apes is flimsy. To remedy this situation, this paper offers an extensive survey and thorough discussion of the ossification of the posterior border of the sphenoid greater wing. Indeed, this area provides much information about basicranial skeletal maturation. We investigate three variants: the absence of the foramen spinosum and the position of both the foramen spinosum and the foramen ovale in relation to the sphenosquamosal suture. Providing original data about humans and 1,425 extant great ape skulls and using a sample of 64 fossil hominids, this study aimed to test whether different ossification patterns occurred during the course of human evolution.

The incidence of three derived morphologies located on the posterior border of the sphenoid greater wing increases during human evolution at different geological periods. The evolutionary polarity of these three derived morphologies is assessed by outgroup comparison and ontogenetic methods. During human evolution, there is a clear trend for the foramen spinosum to be present and wholly located on the posterior area of the sphenoid greater wing. Moreover, in all the great ape species and in *Australopithecus afarensis*, the sphenosquamosal suture may split the foramen ovale. Inversely, the foramen ovale always lies wholly within the sphenoid greater wing in *Australopithecus africanus*, robust australopithecines, early *Homo*, *H. erectus* (and/or *H. ergaster*), and *Homo sapiens*. From ontogenetic studies in humans, we conclude that, during human evolution, the ossification of the posterior area of the sphenoid greater wing progressively surrounded the middle meningeal artery (passing through the foramen spinosum) and the small meningeal artery (passing through the foramen ovale). Am J Phys Anthropol 107:387–399, 1998.

Differential cranial skeletal maturation patterns are observed in extant humans and the chimpanzee species when large samples are considered. These comparative data are essential to understand more in depth fossil

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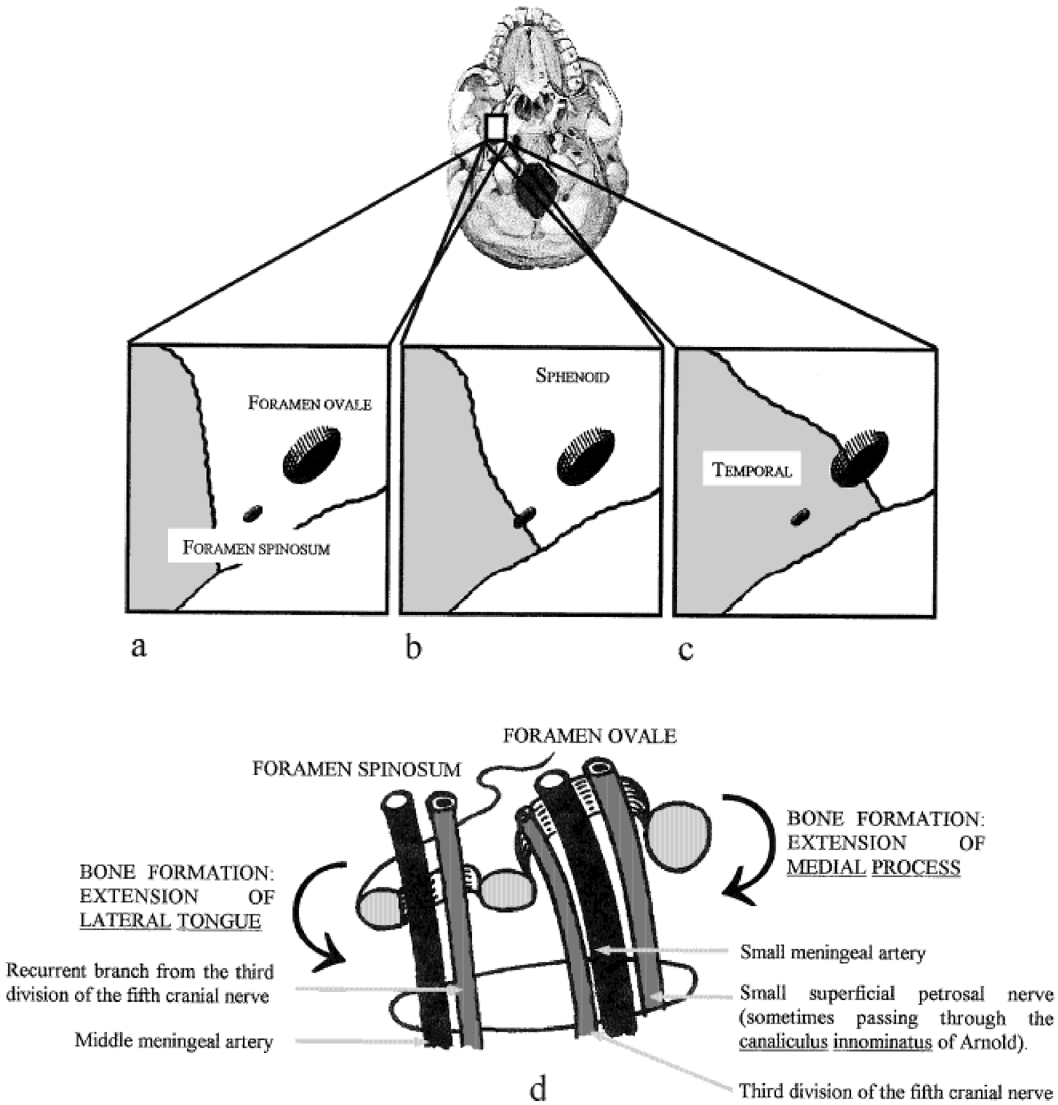

Fig. 1. Position of both foramen ovale and foramen spinosum in relation to the sphenosquamosal suture. **a:** Foramina ovale and spinosum wholly on the sphenoid greater wing. **b:** Foramen spinosum on the sphenosquamosal suture and foramen ovale of the sphenoid bone. **c:** Foramen spinosum of the squamous part of the temporal bone and foramen ovale on the sphenosquamosal suture. **d:** Drawing of a right greater wing in a human embryo viewed posterolaterally. Note the lateral tongue and the broader medial process progressively developing around the small meningeal artery.

hominid growth patterns (Braga, 1998). In this respect, many variants related to ossification may occur in the posterior border of the sphenoid greater wing.

The location of both the foramen ovale and the foramen spinosum (Fig. 1a–c) has drawn the attention of many investigators. For example, when Broom (1946:52) described Sts 5, an adult representative of *Australopithecus africanus,* he wrote, "as a considerable part of the sphenoid lies outside the foramen ovale the condition in this region is distinctly more man-like." Tobias (1967, 1991) widely contributed to the study of this area in detecting a graded series from *Australopithecus* to modern *Homo sapiens.* He

defined different stages in this series by examining carefully the topographic relationships between the entoglenoid process, the sphenoid spine, and the closely related foramen spinosum. With respect to the location of both the foramen ovale and the foramen spinosum, Tobias (1967:40) distinguished two distinct factors: a "tendency of the mandibular fossa with its contained condylar process to expand in certain hominoids and to become smaller in others" and a "tendency towards lateral expansion of the alisphenoid with hominisation, the sphenosquamous suture developing progressively more laterally and successively engulfing the foramen ovale, foramen spinosum and, ultimately, part or all of the entoglenoid process." Tobias (1967:40) found that this latter tendency "is just evident in the australopithecines, the foramen ovale alone having been engulfed by the alisphenoid."

In humans, the foramen ovale lies wholly on the sphenoid greater wing, whereas the foramen spinosum is located on the sphenoid spine. The foramen ovale carries the third division (or mandibular branch) of the fifth cranial nerve, the small meningeal artery, and sometimes the small superficial petrosal nerve (sometimes passing through the canaliculus innominatus of Arnold) (Fig. 1d). The foramen spinosum transmits the middle meningeal artery and a recurrent branch from the third division of the fifth cranial nerve (Fig. 1d).

However, in extant great apes as well as in early hominids, the term *foramen spinosum* is used with reference to human anatomy, but in fact either this foramen is not systematically located on the sphenoid spine or this spine does not necessarily exist. In this connection, describing the *Homo erectus* skull from Salé, Hublin (1991:186) goes on to write, "la présence d'une épine du sphénoïde, absente chez les *Homo erectus* africains et asiatiques est un caractère dérivé commun avec *Homo sapiens*." In extant great apes and fossil hominids, the foramen ovale may be partly located on the squamous part of the temporal bone. Moreover, the foramen spinosum may be either confluent with the foramen ovale (Le Double, 1903) or posteriorly delimited by the petrous part of the temporal bone. The foramen ovale is ossified by bone formation around the opening by the meeting of the extensions of a lateral tongue and a medial process (Fig. 1d). These elements are mesenchymatous in the younger specimen and bony parts of the membranous alisphenoid in the older (James et al., 1980). James et al. (1980:102) noted that "the contribution to the adult sphenoid derived from the medial process includes the relatively slender bar of bone seen from dorsally as the posteromedial margin of the foramen ovale." The completion of the foramen ovale may never take place (Edinger and Kitts, 1954). Thus, the posterior delimitation of the foramen ovale appears highly variable (Kier et al., 1976; Sasaki and Kodama, 1976). The lateral tongue becomes the base of the sphenoid spine. However, the bulk of this spine may be formed by apposition "just below the tip of the tongue to carry the middle meningeal artery posterolaterally away from foramen ovale, buttressed by a very substantial contribution growing in a posterior and medial direction from the more lateral part of the greater wing" (James et al., 1980:102). Interestingly, Deniker (1886) noted that, in a gorilla fetus, the posterior delimitation of the foramen ovale was incomplete. Moreover, in humans and, to a large extent, in great apes, the foramen spinosum is an inconstant foramen. James et al. (1980: 95) observed that the variations observed in this area "may reflect the junctions between distinct embryonic components."

Until now, relevant studies have focussed on a few fossil hominids and small samples of extant great apes. The maturation of the posterior border of the sphenoid greater wing does not seem to have been considered in these words, though some variations of both foramen spinosum and foramen ovale may be achieved through disturbances in ossification. Accordingly, the aim of this study is, first, to provide original data about extant great apes by investigating 1,425 specimens. Second, by using our original comparative data and discussing data about 64 fossil hominids, we will test whether different ossification patterns occurred during the course of human evolution. The following three features will be studied and interpreted: the presence/absence of the foramen spinosum and the position of both the fora-

men spinosum and the foramen ovale in relation to the sphenosquamosal suture passing on their lateral margin. We note that we score the sphenosquamosal suture intercepting a foramen (ovale or spinosum) exclusively when the foramen is clearly bordered, even partly, by the squamous part of the temporal bone. Distinctly, in many cases, the sphenosquamosal suture passes close to the foramen, and its lateral margin is formed by a very thin lamina of sphenoid bone. In such cases, the foramen is scored as wholly sphenoidal.

MATERIAL AND METHODS

To examine the ossification pattern in humans, we employed the data published by Sasaki and Kodama (1976). We also examined 25 skulls from the Spitalfields collection, ranging in age from birth to 19 years. In order to obtain a satisfactory picture of geographical variation in extant great apes, we studied skulls of 1,425 specimens from the following species: 528 *Pan troglodytes,* 162 *Pan paniscus,* 394 *Gorilla gorilla,* and 341 *Pongo pygmaeus.* Sixty-four fossil hominids of the following taxa were studied: four *Australopithecus afarensis,* five *Australopithecus africanus,* four *A.* (*Paranthropus*) *robustus,* seven *Australopithecus* (*Paranthropus*) *boisei,* seven early *Homo,* 12 *Homo erectus* (and/or *Homo ergaster*), four "archaic" *Homo sapiens,* three early *Homo sapiens sapiens,* and 18 *Homo sapiens neanderthalensis.* When originals or casts were not available, we used data from the literature (Table 1).

Taxonomic differences were assessed using the appropriate contingency table analysis: Pearson's Chi-square statistics or Fisher's exact tests, if the contingency table had insufficiently large frequencies. All tests were performed using the STATISTICA software package. In order to derive frequencies, we divided the total number of times the trait occurred on either side by the number of sides on which the trait could be observed.

RESULTS

Location of the foramen ovale

Before birth, in both humans and extant great apes, the ossification of the posterolateral margin of the foramen ovale is never completed (Fig. 2). Kier et al. (1976) report that in humans the ossification of this area may be incomplete at 4 years of age. In our human sample (Spitalfields), ossification was completed in less than five cases out of ten in children under 4 years. In extant great apes mainly, the posterolateral border of the foramen ovale is formed by the squamous part of the temporal bone. The sphenosquamosal suture intercepts the foramen ovale on its lateral margin (Fig. 3). The absence of the medial bony wall of the foramen ovale, communicating with the sphenopetrosal fissure (known as the foramen ovale incompletum), which was described in detail by Hauser and De Stefano (1989) in their reference text about discrete or nonmetrical variants and by Crubézy (1991), was not scored in this study. As noted in Table 2, the sphenosquamosal suture intercepting the foramen ovale is predominantly seen in the pygmy chimpanzee (*P. paniscus*) and the gorilla (*G. gorilla*). This is almost the only morphology observed in the common chimpanzee (*P. troglodytes*) and the orangutan (*P. pygmaeus*) (Table 2). We found the highest incidence for the foramen ovale wholly located on the sphenoid greater wing in the gorilla (Table 2).

As in adult humans, the foramen ovale lies wholly on the sphenoid greater wing in all fossil hominids except in one specimen regarded as an *A. afarensis* representative (Table 2). Indeed, one specimen from the Hadar Pliocene deposits (A.L. 333–105) evinces, on the left side, the commonly observed great ape morphology (i.e., the sphenosquamosal suture splitting the foramen ovale). We should add that A.L. 333–105 is a partial juvenile cranium that appears dentally to be almost 2 years younger than the Taung child (Kimbel et al., 1982). Concerning the location of the foramen ovale in L 894–1, an adult fragmentary hominid cranium from the Shungura Formation in the lower Omo basin dating from 1.8 to 1.9 myr is of great interest. Boaz and Howell (1977) note that, on the preserved left side of this specimen, the sphenosquamosal suture splits the anterolateral margin of the foramen ovale. One of us (J.B.) recently examined this specimen. Our observation differs from

TABLE 1. Topographic relationships between the foramen ovale, the foramen spinosum, and the sphenosquamosal suture in fossil hominids

Specimen	Taxon	FS-R	FS-L	FO-R	FO-L	Reference
A.L. 58-22	*A. afarensis*	SSS	SSS[15]	SPH[14]	—	Braga, personal observation (original); Kimbel et al. (1982)
A.L. 166-9	*A. afarensis*	—	SSSQU	—	—	Johanson and Coppens (1976)
A.L. 333-45	*A. afarensis*	SPH	SPH[15]	SPH[15]	SPH[15]	Braga, personal observation (original); Kimbel et al. (1982)
A.L. 333-105	*A. afarensis*	SSS	SSS	SPH	SSS	Braga, personal observation (original)
MLD 37/38	*A. africanus*	SPH	SPH	SPH	SPH	Braga, personal observation (original)
STS 5	*A. africanus*	—	—	SPH	SPH	Braga, personal observation (original)
STS 19	*A. africanus*[1]	—	SPH	SPH	SPH	Braga, personal observation (original)
STS 25	*A. africanus*	—	—	—	SPH	Braga, personal observation (original)
STS 71	*A. africanus*[2]	—	—	SPH	—	Braga, personal observation (original)
SK 47	*A.(P.) robustus*	—	SSS	—	—	Braga, personal observation (original)
SK 48	*A.(P.) robustus*	—	—	SPH	—	Braga, personal observation (original)
SKW 11	*A.(P.) robustus*	—	SPH	—	SPH	Braga, personal observation (original)
TM 1517a	*A.(P.) robustus*	—	SSS	—	SPH	Braga, personal observation (original)
OH 5	*A.(P.) boisei*	SQU	SQU	SPH	SPH	Tobias (1967)
KNM-ER 406	*A.(P.) boisei*	SPH[15]	SPH	SPH	SPH	Braga, personal observation (original); Leakey et al. (1971)
KNM-ER 407	*A.(P.) boisei*	—	—	—	SPH[14]	Braga, personal observation (original); Day et al. (1976)
KNM-WT 17000[3]	*A.(P.) boisei*	SSS	SSS	SPH	SPH	Braga, personal observation (original)
KNM-WT 17400	*A.(P.) boisei*	—	SSS	SPH[14]	SPH	Braga, personal observation (original); Leakey and Walker (1988)
KNM-ER 23000	*A.(P.) boisei*	SSS	—	—	—	Brown et al. (1993)
OMO 323-1976	*A.(P.) boisei*	SSS	—	SPH	—	Braga, personal observation (original)
L 894-1 (z)	*H. habilis*[4]	—	SSS	—	SPH[14]	Braga, personal observation (original); Boaz and Howell (1977)
KNM-ER 1470	*H. rudolf*[5]	SSS[14]	—	SPH	SPH	Braga, personal observation (original); Day et al. (1975)
KNM-ER 1805	*H. habilis*[6]	—	—	SPH	SPH	Braga, personal observation (original)
KNM-ER 1813	*H. habilis*[5]	SPH	SPH	SPH	SPH	Day et al. (1976)
OH 13	*H. habilis*	SSS	SSS	SPH	SPH	Tobias (1991)
OH 24	*H. habilis*	SSS	SSS	SPH	SPH	Tobias (1991)
SK 27	*H. sp.*[7]	—	SSS	—	SPH	Braga, personal observation (original)
SK 847	*H. erectus*[8,10]	—	SPH	—	SPH	Braga, personal observation (original)
KNM-ER 3733	*H. erectus*[8,9]	—	—	SPH	SPH	Braga, personal observation (original)
KNM-ER 3883	*H. erectus*[9]	SSS	—	SPH	SPH	Braga, personal observation (original)
OH 9	*H. erectus*[8,9]	SPH	—	SPH	—	Rightmire (1979)
KNM-WT 15000	*H. erectus*[9]	SSS[14]	SPH	SPH	SPH	Braga, personal observation (original); Walker and Leakey (1993)
Zhoukoudian II	*H. erectus*[11]	—	—	SPH	SPH	Weidenreich (1943)
Zhoukoudian V	*H. erectus*[12]	—	SSS	—	—	Weidenreich (1943)
Zhoukoudian III	*H. erectus*[13]	—	SPH	—	SPH	Black (1931)
Solo VI	*H. erectus*	SPH	SPH	SPH	SPH	Weidenreich (1951)
Solo XI	*H. erectus*	SPH	SPH	SPH	SPH	Weidenreich (1951)
Sangiran IV	*H. erectus*	SPH	—	SPH	—	Elyaqtine, personal observation (cast)
Hathnora	*H. erectus*	—	—	SPH	—	de Lumley and Sonakia (1985)
Broken Hill 1	A. *H.s.*	SPH	SPH	—	—	Elyaqtine, personal observation (original)
Jebel Irhoud I	A. *H.s.*	SPH	SPH	—	—	Elyaqtine, personal observation (original)
Jebel Irhoud II	A. *H.s.*	SPH	—	—	—	Hublin (1991)
Salé	A. *H.s.*	SPH	SPH	SPH	SPH	Hublin (1991)
Skhul V	*H.s.s.*	SPH	SPH	SPH	SPH	Piveteau (1957)
Qafzeh 9	*H.s.s.*	SPH	SPH	—	—	Vandermeersch (1981a)
Qafzeh 11	*H.s.s.*	—	—	SPH	—	Tillier (1984)
Saccopastore 2	*H.s.n.*	SPH	—	—	—	Elyaqtine, personal observation (original)
Steinheim	*H.s.n.*	SPH	SPH	SPH	—	Adam (1985)
Krapina 1	*H.s.n.*	—	SPH	—	—	Elyaqtine, personal observation (original)
Krapina 3	*H.s.n.*	SPH	—	—	—	Elyaqtine, personal observation (original)
Krapina 5	*H.s.n.*	SPH	—	—	—	Elyaqtine, personal observation (original)
Krapina 38.7	*H.s.n.*	SPH	—	SPH	—	Elyaqtine, personal observation (original)
Krapina 39.1	*H.s.n.*	—	SPH	—	SPH	Elyaqtine, personal observation (original)
Tabun I	*H.s.n.*	SPH	SPH	—	—	Elyaqtine, personal observation (original)
Shanidar V	*H.s.n.*	—	SPH	—	SPH	Elyaqtine, personal observation (cast)
Spy 1	*H.s.n.*	SPH	SPH	SPH	—	Elyaqtine, personal observation (photograph)
Spy 2	*H.s.n.*	SPH	SPH	SPH	—	Elyaqtine, personal observation (photograph)

(continued)

TABLE 1. (continued)

Specimen	Taxon	FS-R	FS-L	FO-R	FO-L	Reference
La Ferrassie 1	*H.s.n.*	—	SPH	—	SPH	Elyaqtine, personal observation (original)
La Ferrassie 2	*H.s.n.*	SPH	—	—	—	Elyaqtine, personal observation (original)
La Chapelle aux S.	*H.s.n.*	SPH	SPH	—	—	Elyaqtine, personal observation (original)
La Quina H27	*H.s.n.*	SPH	—	—	—	Elyaqtine, personal observation (original)
La Quina H5	*H.s.n.*	SPH	SPH	SPH	—	Elyaqtine, personal observation (original)
Gibraltar 1	*H.s.n.*	SPH	—	—	—	Elyaqtine, personal observation (original)
Gibraltar 2	*H.s.n.*	SPH	—	—	—	Elyaqtine, personal observation (original)

A., Australopithecus; A. *H.s.,* Archaic *Homo sapiens;* FO, foramen ovale; FS, foramen spinosum; *H., Homo; H.s.n., Homo sapiens neanderthalensis; H.s.s., Homo sapiens sapiens;* L, left; *P., Paranthropus;* R, right; *rudolf., rudolfensis;* SPH, on the sphenoid greater wing; SQU, on the squamous part of the temporal bone; SSS, on the sphenosquamosal suture; SSSQU, either on the sphenosquamosal suture or on the squamous part of the temporal bone.

[1] Kimbel and Rak (1993:478) consider that Sts 19 is "attributable to a second species, apparently of the genus *Homo*."

[2] Clarke (1988) suggests that the variation he observes within the Sterkfontein's Member 4 *A. africanus* sample represents two species: *A. africanus* (including Sts 5), with smaller teeth, and another hominid (including Sts 71), with larger teeth, "ancestral to and directly on the lineage of *Paranthropus*" (Clarke, 1988:291).

[3] KNM-WT 17000, foramen spinosum incompletum observed on both sides by J.B.

[4] Boaz and Howell (1977:105) consider that "the morphology of L.894-1 most closely parallels Old.Hom.24 and Old.Hom.13."

[5] According to Wood (1991), Kimbel and Rak (1993).

[6] According to Wood (1991).

[7] Clarke (1977a:49) considers that "SK 27, which shows no specifically *Paranthropus* characters, is a child belonging to the genus *Homo*."

[8] The species name "*Homo leakeyi*" was given by Heberer (1963) to OH 9. Clarke (1994:190) believes that "OH 9 calvaria could be a male of the same species to which SK 847 and KNM-ER 3733 are females."

[9] Some authors (Andrews, 1984; Stringer, 1984) support the exclusion of all East African forms from the hypodigm of *H. erectus,* while Wood (1984) and Groves (1989) retain OH 9 in *H. erectus* sensu stricto. Wood (1992) argues that KNM-ER 3733, KNM-ER 3883, and KNM-WT 15000 represent *H. ergaster* rather than *H. erectus.* Chamberlain (1989) and Rightmire (1990, 1992) refer these specimens to early *H. erectus.*

[10] Clarke on page 221 of his thesis on SK 847 (Clarke, 1977b) states, "There is no sign of foramen spinosum and the only place it could have been is at the posterior end of the spheno-squamosal suture, lateral to the spine of the sphenoid. Here there is some slight damage to the base on both the infratemporal and cerebral surfaces."

[11] Zhoukoudian II, described as skull of locus D by Black (1931).

[12] Zhoukoudian V, described as "Skull III" by Weidenreich (1935), is of great interest because it was found in locus H which appears, geologically and faunally, of a later age.

[13] Zhoukoudian III, Described as skull of locus E by Black (1931).

[14] Scoring diverging from the original description of the fossil cited in parentheses.

[15] Not scored by the authors but described in the original description cited in parentheses.

Boaz and Howell's description, as we observed the suture passing about 2 mm from the posterolateral margin of the foramen ovale. The latter is wholly alisphenoidal.

Zuttiyeh, an archaic *H. sapiens* (Vandermeersch, 1981b) dated to the Middle Pleistocene (the latest estimate is between 250 and 350 kyr [Sohn and Wolpoff, 1993]), is also interesting with respect to the foramen ovale. Keith (1927:91) noted that, on the posterior border of the right sphenoid greater wing, "the passage for the [third division of the fifth cranial] nerve" (i.e., the foramen ovale) forms "a notch on the hinder margin of the alisphenoid." He added that "it may happen in anthropoid apes." This description (and its illustration on Keith's Figure 26) of the medial wall of the foramen ovale clearly corresponds to a foramen ovale incompletely communicating to some degree, by a narrow or more pronounced aperture, with the medially located foramen lacerum. This feature has nothing to do with the location of the foramen ovale in relation to the sphenosquamosal suture passing on its lateral margin (Braga, 1995). This feature is frequently found in studies dealing with "discrete" or "intrinsically innocuous minor skeletal variants of the human skull" (Hauser and De Stefano, 1989:1). Unfortunately, in Keith's description of the Zuttiyeh skull, there is no mention of the location of the sphenosquamosal suture in relation to the lateral margin of the foramen ovale. This feature is not found in skeletal biological studies based upon analysis of cranial nonmetrical (or discrete) traits even if it is scorable as present or absent.

Absence of the foramen spinosum

In extant great apes, the absence of the foramen spinosum (or its complete confluence with the foramen ovale), as pointed out by Berry and Berry (1971), is extremely frequent in the orangutan (Table 2). This feature is much more uncommon in the

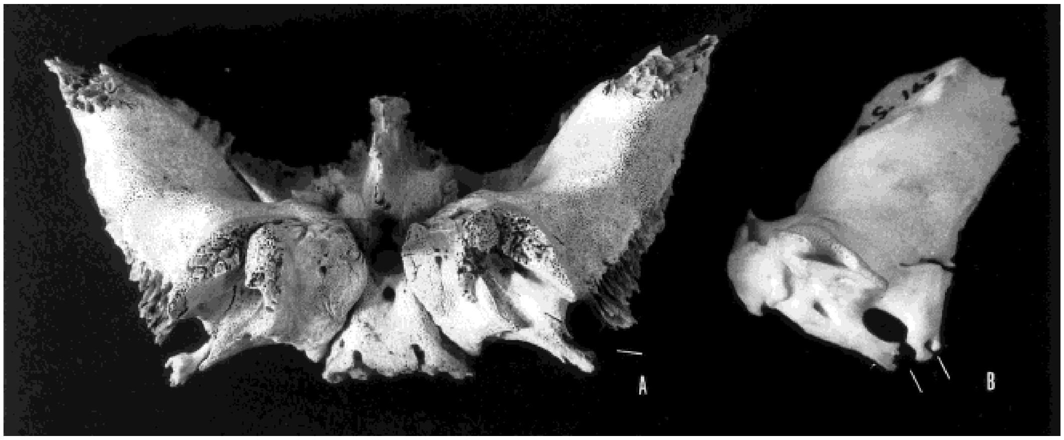

Fig. 2. Inferior view of an infant chimpanzee sphenoid greater wing (**A**) and a human foetus left sphenoid greater wing (**B**). In the chimpanzee sphenoid bone (A), the posterolateral margin of the left foramen ovale is not completed (line). In the human left sphenoid greater wing (B), the extensions of the lateral tongue and the medial process around the foramen ovale are visible (lines). On the right part of the lateral tongue, the posteriorly opened foramen spinosum is visible.

three African ape species. It is rarely observed in extant humans. It was seen only in two (1.6%) of 123 patients with an age range of 1–78 years by Ginsberg et al. (1994). Our data are similar to Falk's (1993) results concerning the orangutan and the pygmy chimpanzee. Our observed frequencies are lower with respect to the gorilla and the common chimpanzee. In extant great apes, as for humans, there is no influence of either age or sex on the incidence of this feature. In the great apes, as for humans, the ossification of the foramen spinosum, when present, is achieved during the first years of life (Braga, 1995).

We never observed the absence of the foramen spinosum in our fossil hominid sample. There is a marked discrepancy between these data and some previous statements. For example, concerning TM 1517, the type specimen of *A.* (*P.*) *robustus* from Kromdraai, Broom (1946:89) wrote, "the lower part of the sphenoid bone has a well developed foramen ovale, but no foramen spinosum. In this *Paranthropus* agrees with the anthropoids, and differs from man." In fact, we believe that in fossil hominids and especially in robust australopithecines the foramen spinosum may be deeply recessed within the cranial base. A groove may extend its inferior (or extracranial) opening. This groove channels the bone (at the level of either the sphenoid greater wing or the squamous part of the temporal bone) in varying degrees of depth, width, and length. The margins bordering this groove may be more or less prominent. Tubercles or spines may project from them, and osseous connections may convert the groove into a canal. This groove is clearly visible on the left side in TM 1517. In this specimen, the groove is open medially at the level of the posterior part of the sphenoid greater wing and extends inferiorly the deeply recessed foramen spinosum. This pattern is also present in SKW 11, a robust australopithecine from Swartkrans. The groove is visible 4.5 mm behind the posterior border of the foramen ovale. It extends the inferior opening of the foramen spinosum. From its borders, two converging osseous tubercles (one medial and one posterior) form an osseous bridge that is medially fissured. We also observed this pattern on the left side of L 894–1. Hublin (1991) described this morphology on the *Homo erectus* representative from Salé. He wrote that the left thick bone lamina forming the sphenoid spine is medially grooved and thereby extends inferiorly the foramen spinosum.

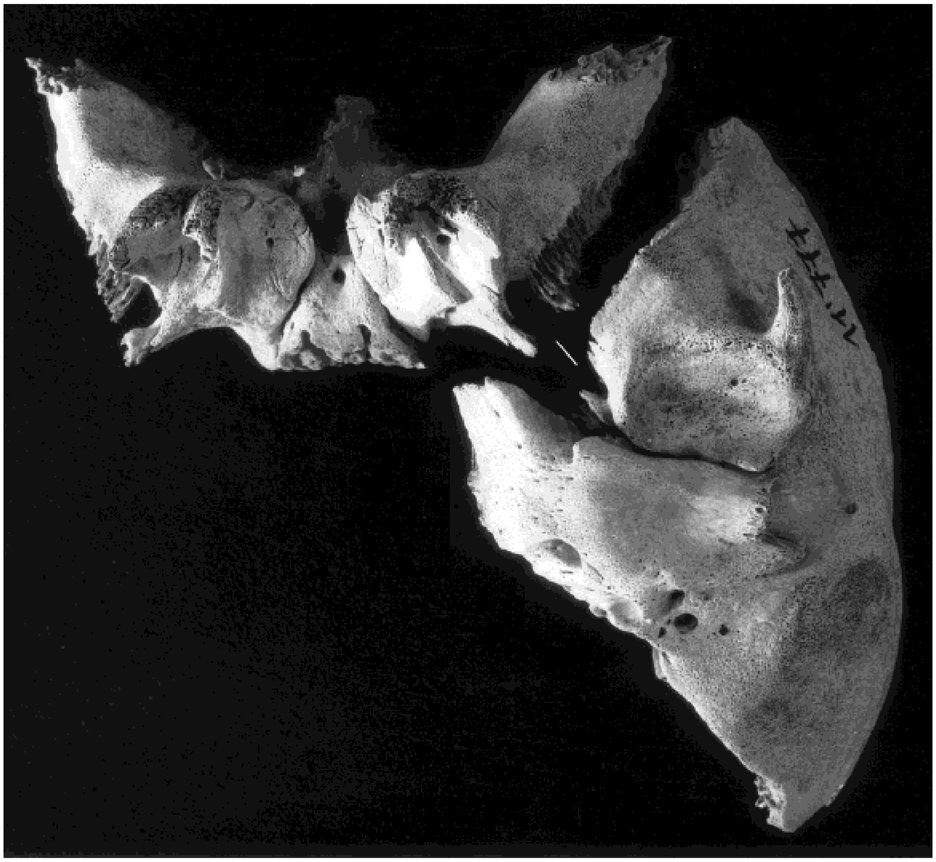

Fig. 3. Inferior view of the sphenoid and the left temporal bones in an infant chimpanzee. The posterolateral border of the left foramen ovale (line) is formed by the squamous part of the temporal bone.

TABLE 2. Frequencies for the presence/absence of the foramen spinosum and the position of both foramen spinosum and foramen ovale in relation to the sphenosquamosal suture[1]

	1	2	3	4	5	6
Pan troglodytes	97.3	2.7	14.6	6.6	74.5	4.3
Pan paniscus	82.1	17.9	9.2	19.6	70	1.2
Gorilla gorilla	73.9	26.1	27.8	36.5	35.2	0.5
Pongo pygmaeus	95.3	4.7	84.1	2.3	9.4	4.2

1, Foramen ovale on the sphenosquamosal suture; 2, foramen ovale wholly of the sphenoid greater wing; 3, foramen spinosum absent; 4, foramen spinosum wholly on the sphenoid greater wing; 5, foramen spinosum on the sphenosquamosal suture; 6, foramen spinosum of the squamous part of the temporal bone.

Location of the foramen spinosum

In humans, the foramen spinosum generally lies wholly on the sphenoid greater wing. In extant great apes, the location of the foramen spinosum, when present, is highly variable (Table 2). The absence of the medial bony wall of the foramen spinosum which allows communication with the sphenopetrosal fissure (foramen spinosum incompletum), described in detail by Hauser and De Stefano (1989) and Crubézy (1991), was not scored in this study. Ginsberg et al. (1994) observed this feature in 33 (26.8%) of their patients. This feature is independent upon the location of the foramen ovale. In most chimpanzee skulls, the foramen spinosum is located on the sphenosquamosal suture. In gorilla skulls, this foramen lies either on the sphenosquamosal suture or on the sphenoid greater wing. The orangutan is unique among the great apes because in this species the foramen spinosum is usually absent. In all the great ape species, the

foramen spinosum rarely lies on the squamous part of the temporal bone.

In all the fossil *H. sapiens* representatives (including Neandertals), the foramen spinosum lies wholly within the sphenoid greater wing. In *H. erectus* (and/or *H. ergaster*), this foramen lies on the sphenosquamosal suture in three cases out of 12 (25%). In two specimens (KNM-ER 3883 and Zhoukoudian V), the sphenosquamosal suture splits the foramen spinosum on the only preserved side (Table 1). In KNM-WT 15000, both morphologies are scored. In earlier representatives of the genus *Homo*, the foramen spinosum may be seen on the sphenoid greater wing (KNM-ER 1813, SK 847), or on the sphenosquamosal suture (OH 13, OH 24, KNM-ER 1470, SK 27, and L 894–1) in seven cases out of nine (78%). In robust australopithecines, we observed a high variability in the location of the foramen spinosum, and the different patterns are present (Table 1). In seven cases out of 12 (58%), the foramen spinosum lies on the sphenosquamosal suture. The foramen spinosum was preserved in only two *A. africanus* representatives. In both of them, the foramen spinosum lies wholly on the sphenoid greater wing. On the right side, one of these two specimens—MLD 37/38—evinces a 4 mm long cleft extending between the foramen ovale and the foramen spinosum. This feature is certainly due to the persistence of an immature state, described as foramina ovale et spinosum confluens (Braga, 1995). Finally, in *A. afarensis*, the foramen spinosum is frequently seen on the sphenosquamosal suture (five cases out of seven [71%]), a situation frequently evinced in early *Homo*.

The difference in the location of the foramen spinosum between these two groups, however, is not statistically significant at all ($\chi^2 = 0.08$; df = 1; $P = 0.7711$). The difference does become significant between *A. afarensis* and either *H. erectus* ($\chi^2 = 3.91$; df = 1; $P = 0.0480$) or *H. sapiens* (Fisher's exact test; one-tailed and two-tailed $P = 0.0001$). When we considered robust australopithecines and early *Homo*, two groups preserving a large number of foramen spinosums, interesting results emerged. While not significant between *H. erectus* and robust australopithecines ($\chi^2 = 2.74$; df = 1; $P = 0.0977$), the difference is significant between this latter group and *H. sapiens* (Fisher's exact test; one-tailed and two-tailed $P = 0.0000$). The difference between early *Homo* and either *H. erectus* ($\chi^2 = 5.74$; df = 1; $P = 0.0166$) or *H. sapiens* (Fisher's exact test; one-tailed and two-tailed $P = 0.0000$) is statistically significant. Finally, the difference between *H. erectus* and *H. sapiens* is also significant ($\chi^2 = 7.57$; df = 1; $P = 0.0059$).

DISCUSSION

The absence of the foramen spinosum and the occurrence of the foramen ovale on the sphenosquamosal suture are much more frequently found in extant great apes, regarded as the outgroup, than either in humans or in fossil hominids. Moreover, depending on the feature considered, some fossil hominids display either a primitive or a derived pattern. The reformulation of the biogenetic law by Nelson (1978) can be used here to validate the outgroup comparison. As noted previously, during ontogeny the posterior border of the foramen ovale is not ossified before 4 years of age. During ontogeny, the foramen ovale ossifies by bone formation around the opening by the meeting of the mesenchymatous extensions of a lateral tongue and a medial process (Fig. 1d). The foramen spinosum also ossifies by bone formation around the middle meningeal artery from the lateral tongue (Fig. 1d). Given this ontogenetic character transformation, the presence of the foramen ovale and/or the foramen spinosum on the sphenosquamosal suture or their confluence, reflecting an incomplete alisphenoidal ossification, are observed to be more general, and the presence of both foramina on the sphenoid greater wing is observed to be less general (Nelson, 1978). We should regard the more general morphologies as the persistence of immature morphologies (Fig. 2). Indeed, in humans as in extant great apes, according to Ossenberg's classification (1969), these variants are hypostotic traits.

An important difference between the orangutan (to be considered as the sister group of the African ape–hominid clade) and the Afri-

can apes was established on the presence of the foramen spinosum. This foramen is rare in the orangutan. Inversely, it is always present in humans and all fossil hominids. Moreover, during human evolution, there is a clear trend for the foramen spinosum to be mostly located on the sphenoid greater wing. In humans and all the *H. sapiens* representatives (Table 1) with subsequent ossification, both foramen ovale and foramen spinosum are sphenoidal. The occurrence of the foramen spinosum on the sphenoid greater wing decreases from the late *H. erectus* to the early *A. afarensis*.

Mostly, in extant great apes, the sphenosquamosal suture splits the foramen ovale. Inversely, this morphology is never observed in the *Homo* lineage, in *A. africanus* known from about 3 (Makapansgat) to 2.4 (Gladysvale) myr, and in robust australopithecines, including the earliest known yet (i.e., KNM-WT 17000 and OMO 323–1976) (Table 1). Interestingly, in an *A. afarensis* representative (AL 333–105), the sphenosquamosal suture splits the foramen ovale. This variation in the course of the sphenosquamosal suture in *A. afarensis* is in strong contrast with the pattern observed in all the geologically younger fossil hominids. This means that in *A. afarensis* a primitive morphology reflecting an incomplete ossification of the posterior border of the sphenoid greater wing may be present. This primitive morphology is absent in all the 26 Pliocene and Plio-Pleistocene hominids dated from about 3 to 1.5 myr scored in this study. Given the character polarity determined by both the outgroup comparison and the ontogenetic methods, the split of the foramen ovale by the sphenosquamosal suture occurring at various proportions may correspond to a primitive feature shared by *A. afarensis* and its ancestor in the hominid lineage. Moreover, even if additional data concerning *A. anamensis* and *Ardipithecus ramidus* would be very useful to confirm this hypothesis, we believe that the variability in the location of the foramen ovale disappeared in the *Homo* and robust australopithecines lineages as soon as 2.5 myr.

Our original data for fossil hominids and extant great apes confirm Tobias's belief (1967, 1991) that the posterior border of the sphenoid greater wing is a key area in the study of fossil hominids. We conclude that during the course of human evolution the ossification of the posterior border of the sphenoid greater wing progressively developed around the middle meningeal artery (passing through the foramen spinosum) and the small meningeal artery (passing through the foramen ovale). The recent findings by Rak et al. (1996) about the shape of the crescent of foramina (superior orbital fissure, foramen rotundum, foramen ovale, and foramen spinosum) on the sphenoid bone are peculiarly interesting. They conclude that *A. afarensis* from Hadar "shares much of the morphology of this region with the African great apes" (Rak et al., 1996:93). This morphology concerns the shape of the superior orbital fissure and its close proximity to the foramen rotundum. These findings are congruent with our results for two reasons. First, they confirm the primitive morphology we observed in *A. afarensis* concerning the location of the foramen ovale. Second, they confirm our opinion about the persistence of an immature morphology, consisting of incomplete alisphenoidal ossification, in *A. afarensis*. Indeed, Rak et al. (1996:97) observed a "very thin bridge between the superior orbital foramen and the foramen rotundum" in the adult A.L. 417–1 and the infant A.L. 333–105 *A. afarensis* specimens. They added that "in early ontogenetic stages modern humans exhibit an even larger and more extensive superior orbital fissure than do adults" (Rak et al., 1996:97). Thus, as in the present study, Rak et al. (1996) reach the same conclusion by the outgroup and ontogenetic methods.

We should add that the morphology of the posterior border of the sphenoid greater wing also depends on the composition of the vascular network and its the branching in relation to the position of bone. For example, Ginsberg et al. (1994:289) already observed that "congenital variants of the foramen spinosum are generally related to defects in osteogenesis or to maldevelopment of the middle meningeal artery." The foramen spinosum transmits the middle meningeal artery, a branch of the maxillary artery that

stems from the maxillary ramus of the external carotid artery. From dissections of cephalic arteries (Muller, 1977; Diamond, 1988) and from the analysis of endocasts (Falk, 1993), previous studies found that branches of the internal carotid artery (entering through the superior orbital fissure or the cranio-orbital foramina) may supply the meningeal arteries of the middle cranial fossa. This pattern is rarely observed in humans. Interestingly, in extant great apes, Falk (1993) found a correspondence between low frequencies of external carotid dominance and low frequencies for the presence of the foramen spinosum. Moreover, Falk (1993:93) added that "Sinanthropus was apelike rather than humanlike in that a relatively high frequency of the meningeal arteries that supply portions of the middle braincase stemmed from the orbit rather than the floor of the middle cranial fossa." With regard to the presence of the foramen spinosum, as we find a human-like pattern in all the fossil hominids, we should question if there is a real functional correspondence between the ossification of the foramen spinosum and the pattern of the meningeal arterial supply. We should also add that other vascular variations may explain the absence of a foramen spinosum. For example, Curnow (1873) described hypoplasia of the foramen spinosum in association with the origin of the middle meningeal artery from the ophthalmic artery.

CONCLUSIONS

The aim of this study was to assess the variation of three features associated with the ossification of the posterior border of the sphenoid greater wing in a large sample of extant great apes. Whether different patterns of ossification occurred during the course of human evolution was tested by using a sample of 64 fossil hominids. Doing so, we demonstrate a clear trend for the foramen spinosum to be present and wholly located on the posterior area of the sphenoid greater wing. Another point to be made is that, contrary to later hominids, *A. afarensis* may evince a primitive morphology where the sphenosquamosal suture splits the foramen ovale.

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